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Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf

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au début des années 1990 et n’a montré aucun signe de rétablissement durant les 15 années d
moratoire sur la pêche. Son abondance connaît toutefois, depuis peu, une augmentation. L’absence prolongée d’un rétablissement et l’amélioration récente ont toutes deux été attribuées des changements dans la biomasse de poissons fourrage qui se reflètent dans des effets de la prédation et de la concurrence par ces poissons sur les premières étapes du cycle de vie de la morue. Un examen des relations entre la biomasse de poissons fourrage et la dynamique des populations de morue de l’ESS n’a fourni aucun appui à cette hypothèse. Contrairement à ce qu cette dernière prédit, le taux de recrutement de morues n’était pas relié à la biomasse de poissc fourrage. Le principal facteur ayant retardé le rétablissement est une mortalité naturelle (*M*) éle des morues adultes. L’amélioration récente du stock de morue de l’ESS est le fait de la forte cla d’âge de 2004 et d’une diminution de la *M*. Ces facteurs ne peuvent être attribués à aucun effet des poissons fourrage. Tant le rétablissement tardif que l’amélioration récente du stock de moru de l’ESS semblent être attribuables à des facteurs autres que les interactions avec les poissons fourrage.

Introduction

Dans cet article

Most stocks of Atlantic cod (*Gadus morhua*) in the Northwest Atlantic collapsed in the early 1990s predominantly because of overfishing. Nearly 20 years later, most of these stocks have failed to re despite severe restrictions on fishing effort. The main cause of failed recovery has been a sharp de in the productivity of these stocks, though continued fishing is also an important factor in some cas (Shelton et al. 2006). The decline in productivity has been most severe for the cod stocks in the so Gulf of St. Lawrence (SGSL) and on the eastern Scotian Shelf (ESS). For these two stocks, avera population growth rates in the absence of fishing have been estimated to be negative during the pe after their collapse (Shelton et al. 2006). Understanding the causes of these severe declines in productivity is a critical first step in determining what additional management actions, if any, would appropriate to promote the recovery of these once important resources.

Walters and Kitchell (2001) suggested that the success of the dominant predatory fishes in an eco may often be partly due to “cultivation effects”, where adults crop down forage fishes that are pred and (or) competitors of their own juveniles. In such cases, depensatory decreases in juvenile surviv would be expected following severe reductions in adult abundance, as forage fish, released from predation, increased in abundance. Walters and Kitchell (2001) argued that this cultivation–depens mechanism may be an important factor in the lack of recovery of cod stocks depleted by overfishin Consistent with this suggestion, negative relationships between cod recruitment success and the b of pelagic forage fishes have been reported for the SGSL (Swain and Sinclair 2000) and for the No Sea (Fauchald 2010). Likewise, a number of studies suggest that recovery of cod in the Baltic Sea be hindered by pelagic forage fishes, both through predation on cod eggs (Köster and Möllmann 2 and through competition with larval cod (e.g., Casini et al. 2009).

Frank et al. (2011) recently reported that cod and other large demersal fishes on the ESS are now recovering towards their precollapse state of ecosystem dominance. They argued that the high bio of planktivorous forage fishes that developed on the Scotian Shelf following the collapse of demers fishes governed the prolonged lack of demersal fish recovery through increased predation on and competition with their early life stages. Likewise, they attributed a recent increase in demersal fish biomass to a decline in forage fishes and the resultant weakening of predation and competition by fishes.

In this paper, we evaluate the hypotheses proposed by Frank et al. (2011) focussing on cod, forme dominant demersal fish in the ESS ecosystem and the species most closely linked to the changes aggregate demersal fish biomass in this system. Based on an examination of the dynamics of the E cod stock, we conclude that neither the delay in the recovery of ESS cod during the moratorium on directed fishing (initiated in September 1993) nor the recent improvement in the status of this stock be attributed to effects of changes in forage fish biomass.

Materials and methods

Dans cet article

Changes in forage fish biomass on the ESS were tracked based on catch rates in an annual bottor survey of this area, conducted each July since 1970. Following Frank et al. (2011), a biomass inde forage fishes was constructed based on the catches of three dominant species: northern sand lanc

(*Ammodytes dubius*), capelin (*Mallotus villosus*), and Atlantic herring (*Clupea harengus*). Catch rates were scaled to "trawlable biomass" by multiplying the stratified mean catch rate by the survey area divided by the area swept by a standard tow. As in Frank et al. (2011), catches of sand lance and capelin were multiplied by 200 and those of herring by 40 to account for the low catchability of these species to the survey gear.

Time series of cod biomass, recruitment success, and mortality were estimated based on the population model used in the most recent assessment of this stock (DFO 2011), updated with survey data for 2010 and 2011 to include the recent cod "recovery" (Supplementary Appendix S1[1]). This model is a sequential population analysis, the standard assessment model used for cod in eastern Canada. Model inputs were annual fishery catches at ages 1 to 15 years and survey catch rates at ages 1 to 10 years. In addition to estimating abundance at age in the most recent year and catchabilities at age to the survey, the model used for ESS cod estimates time trends in the instantaneous rate of natural mortality (*M*) for two age groups, cod aged 1–4 years and those 5 years and older (5+). An example of model fit to the data is shown in Fig. 1*b*.

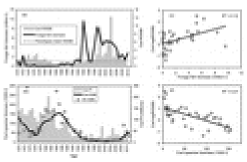

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Fig. 1. Relationships between cod recruitment (*R*, abundance at age 1 year), cod recruitment rate (*R*/SSB), cod spawning stock biomass (SSB), and forage fish biomass on the eastern Scotian Shelf. In panel (*b*), the heavy line shows the model estimate of beginning-of-year cod SSB, and circles show cod SSB based on survey catches (corrected for catchability and projected back to the beginning of year). Recruitment rates are plotted by year class rather than by the year when they were observed as 1-year-olds.

Recruitment rate, the number of age-1 recruits produced per unit of spawning stock biomass (SSB), was used as an index of cod recruitment success. An index of cod condition was calculated using the length (*L*) and weight (*W*) measurements made on cod catches in the annual survey. The predicted weight (g) at L = 60 cm (near the average length of a 7-year-old cod) was calculated using the annual *L*–*W* relationships and expressed as Fulton's K ($100W/L^3$).

Results and discussion

Dans cet article

If high forage fish biomass delayed the recovery of cod through predation on and (or) competition with the early life stages of cod, this should be reflected in low recruitment success for cod during the period of high forage fish biomass. The opposite is observed (Fig. 1*a*). Following the collapse of cod in the early 1990s, cod recruitment rate was above the precollapse average despite high forage fish biomass. Furthermore, the period of high forage fish biomass produced three year classes of cod with very high recruitment rates (the 2000, 2003, and 2004 year classes), two to four times greater than the highest rate observed in the precollapse period of low forage fish biomass.

Over the longer term, there is no indication of a negative effect of forage fish biomass on recruitment rate of ESS cod (Figs. 1*a*, 1*c*). Instead, cod recruitment rate appears to be more closely linked to cod SSB, with recruitment rate showing the expected compensatory increase at low SSB (Fig. 1*d*). Furthermore, residuals from the cod stock–recruit relationship were unrelated to forage fish biomass ($R^2 < 0.005$), and forage fish biomass was not a significant ($P > 0.25$) covariate in cod stock–recruit models (Supplementary Appendix S2[1]). There are a number of reasons why forage fish biomass may not have an important effect on cod recruitment success on the ESS. In other areas where there have been detailed process-oriented studies, the level of consumption of cod eggs and larvae by pelagic fishes has depended strongly on factors such as the species of pelagic fish, the extent of the spatial overlap between pelagic fish and early life stages of cod, and the local abundance of alternate prey for pelagic fish (e.g., Köster and Möllmann 2000; Fauchald 2010 and references therein). Furthermore, McQuinn (2009) has suggested that the increase in the survey index of pelagic fish biomass in the 1990s reflected an increase in the availability of these fishes rather than an increase in their biomass. He argued that increased use of near-bottom habitats by pelagic fishes following the collapse of cod has resulted in increased availability of these fishes to the bottom-trawl gear used in the surveys.

The main factor delaying the recovery of ESS cod has been high *M* (Shelton et al. 2006), in particular *M* of adult (5+) cod (DFO 2011). Estimated *M* of 5+ cod increased sharply in the early 1990s, reaching unprecedented levels (0.8–1.1) over the 1995–2006 period (Fig. 2*a*). Estimated *M* of cod aged 1–4 years was also relatively high (0.50–0.54) from 1993 to 2001, but similar levels also occurred earlier in the mid-1970s and mid-1980s. The period of high *M* of 5+ cod coincided with the period of high forage fish biomass in the survey (Fig. 2*a*). These forage fishes are important prey, not predators or competitors, of large cod (e.g., Bundy and Fanning 2005). Elevated natural mortality of large cod would not be expected to result from a high abundance of their prey. However, Bundy and Fanning (2005) suggested an indirect effect, with poor condition of small cod due to competition with abundant forage fishes carrying over to adults and resulting in elevated *M* of large cod in the late 1990s. For this hypothesis to provide an explanation for elevated *M* of large cod, two relationships need to exist: (*i*) condition of large cod should be negatively related to the biomass of forage fishes at earlier ages when these cod competed with forages fishes, and (*ii*) *M* of large cod should be negatively related to their condition. Neither of these relationships hold true on the ESS (Figs. 2*c*, 2*d*). Instead, condition of large cod was low throughout the 1980s and early 1990s, a period when both forage fish biomass in the survey and 5+ cod *M* tended to be low, and above the long-term average in most years since the mid-1990s, including periods of high forage fish biomass and high 5+ cod *M* (Figs. 2*a*, 2*b*). These relationships are inconsistent with the hypothesis of Bundy and Fanning (2005) and with the notion that the high *M* of 5+ cod since the mid-1990s is a consequence of high forage fish biomass (or poor condition).

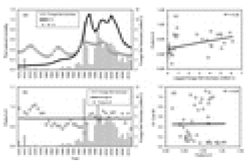

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Fig. 2. Relationships between the instantaneous rate of natural mortality (*M*) of cod aged 1–4 or 5+ years, Fulton's condition factor *K* (based on the weight of a 60 cm cod predicted from annual length–weight relationships), and forage fish biomass (based on survey catch rates). In panel (*c*), forage fish biomass is the average biomass 4 to 7 years earlier; this lag is the interval between cod ages 0–2 years (the ages assumed to compete with forage fishes) and 6–7 years (the probable ages of 60 cm cod).

The recent improvement in the status of ESS cod results mainly from the decline in 5+ *M* from values near 1 to about 0.45 (still over twice the level considered normal for cod) and the strong 2004 year class (Fig. 1*b*). These changes cannot be attributed to effects of a recent decline in forage fish biomass. The 2004 year class was produced when forage fish biomass was still high. The decline in *M* of adult cod cannot be attributed to a decline in the biomass of their prey. Cod condition did not improve during the period of declining 5+ *M*. The hypothesis that the prolonged delay in the recovery of ESS cod and the recent improvement in this stock are being governed by changes in the biomass of forage fishes is therefore not supported by the data.

If the long delay in the recovery of ESS cod cannot be attributed to an effect of high forage fish biomass, what factors may have been important in this delay? A number of authors have suggested that physical environmental forcing played an important role in the decline of cod in the Northwest Atlantic in the late 1980s and early 1990s. For example, Rothschild (2007) suggested that negative environmental conditions affected plankton dynamics, resulting in "a major perturbation in the forage available to cod." Given this hypothesis, the delay in recovery might be attributed to a decline in the abundance or quality of forage available to cod, resulting in an increase in natural mortality due to poor fish condition. This does not appear to be the case for ESS cod because condition of adult cod has been above average since the mid-1990s. The neighbouring cod stock in the SGSL also exhibits very high 5+ *M*, and it has been hypothesized that predation by grey seals (*Halichoerus grypus*) is an important cause of elevated *M* in that stock (references in O'Boyle and Sinclair 2012). Most modelling studies have concluded that predation by grey seals is not an important component of the elevated *M* of adult ESS cod (references in O'Boyle and Sinclair 2012). However, using different model assumptions, O'Boyle and Sinclair (2012) concluded that the increases in *M* of ESS cod have been due in large part to predation by grey seals, though the recent decrease in *M* of ESS cod is inconsistent with their model results. One hypothesis that could account for this reduction in *M* would be prey-switching by grey seals because of a decline in the availability of cod or an increase in the availability of alternate prey. Changes in availability could reflect changes in the behaviour of prey (e.g., a change in cod behaviour to reduce risk of predation) or predators (e.g., a change in the foraging distribution of the far-ranging seal herd) as well as changes in prey abundance.

Footnotes

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/f2012-045.

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